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Artificial light increases local predator abundance, predation rates, and herbivory

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Keywords

artificial light at night (ALAN), phototaxis, human-modified ecosystems, urban ecology, species interactions, predation, herbivory, arthropod, insect

Abstract

Human activity is rapidly increasing the radiance and geographic extent of artificial light at night (ALAN). The timing and characteristics of light affect the development, behavior, and physiological state of many organisms. Depending on the ecological context, plants and animals respond to artificial lights in both adaptive and maladaptive ways. Mesocosm experiments have demonstrated both top-down and bottom-up control of populations under ALAN, but there have been few community-scale studies that allow for spatial aggregation through positive phototaxis, a common phenomenon among arthropods. We performed a field study to determine the effects of ALAN on arthropod communities, plant traits, and local herbivory and predation rates. We found strong positive phototaxis in 10 orders of arthropods, with increased (159% higher) overall arthropod abundance under ALAN compared to unlit controls. The arthropod community under ALAN was more diverse and contained a higher proportion of predaceous arthropods (15% vs 8%). Predation of immobilized flies occurred more 3.6 times faster under ALAN; this effect was not observed during the day. Contrary to expectations, we also observed a 6% increase in herbivory under ALAN. Our results highlight the importance of open experimental field studies for determining the community-level effects of ALAN.

Introduction

Terrestrial organisms nearly ubiquitously use light to gather information about their environment, with most taxa capable of responses to changes in spectral composition, intensity, or duration (Cashmore et al. 1999). Humans frequently modify the light environment in the increasingly broad spaces in which we live and work, with light emittance increasing 2.2% annually worldwide between 2012 and 2016 (Kyba et al. 2017). Light emittance will likely continue to increase as LED's lower the cost of installing and operating lights globally (Pust et al. 2015).

One of the most noticeable effects of artificial light at night (ALAN) is movement toward light sources by arthropods (positive phototaxis) and has been a subject of study for many decades. Positive phototaxis can locally increase the abundance of an arthropod species 20-fold (Eccard et al. 2018), but the opposite effect, negative phototaxis (repellence) is also frequently observed (Owens and Lewis 2018). There have been only a limited number of studies that compare phototaxis within communities of arthropods, and even fewer describing changes in local composition as it relates to trophic

strategy or other life history correlates (Gaston et al. 2015). Even if all nocturnal arthropods were uniformly attracted, nocturnal arthropods are on average larger compared to diurnal communities in the same location and have different trophic strategies (Guevara and Avilés 2013, McMunn and Hernandez 2018). ALAN could lead to “nocturnal enrichment”, a local aggregation of animals biased toward nocturnally active taxa. Nocturnal enrichment would lead to larger average body sizes and differing prevalence of trophic strategies in areas exposed to ALAN. Beyond phototaxis, there are many other ways in which ALAN can directly affect arthropods, with examples of spatial and temporal disorientation, desensitization to light, and changes in pattern recognition ability (Owens and Lewis 2018). These direct effects of ALAN on arthropods can be specific on the basis of size (Heiling and Herberstein 1999), developmental stage (Durrant et al. 2018), or sex (van Geffen et al. 2014).

Plants, like arthropods, have a diversity of responses to ALAN. Light is perhaps most obviously used for photosynthesis among plants, but photoperiod and spectral composition also serve as important daily and seasonal cues. Artificial lights are often bright enough to affect plant physiology (Briggs 2006), phenology (Bennie et al. 2016), form, and resource allocation (Bennie et al. 2016). Earlier or later phenologies, increased or suppressed growth (Cathey and Campbell 1975), decreased flower production (Bennie et al. 2015), and altered leaf toughness (Grenis and Murphy 2018) have all been observed as direct plant responses to ALAN.

While there is an abundance of previous research on responses of individual species to ALAN, there is comparatively less work characterizing how artificial lights affect the composition of ecological communities and species interactions. However, several studies have described how nocturnal predators exploit aggregations of prey items around light sources. For example, bats have increased capture success of moths under lights, not only to due to increased local moth abundance, but also moth disorientation and diminished predator avoidance behaviors (Rydell 1992, Acharya and Fenton 1999). Among web-building spiders, ALAN increases prey catch, with illuminated sites being preferred and occupied by larger spiders (Heiling and Herberstein 1999). Changes in activity time of local fauna can also affect predator abundance, with diurnal cursorial spiders capable of extending foraging duration under ALAN (Peckhamia 2009)

. Increased predator abundances near light sources and other costs of phototaxis presumably reduce moth fitness when lights are common, with selection leading naïve urban moths to display reduced phototaxis compared to their rural counterparts (Altermatt and Ebert 2016).

There are substantially fewer studies that have investigated how artificial lights affect plant-arthropod interactions. Previous studies have shown that plants can have tougher leaves under ALAN, reducing herbivore performance (Grenis and Murphy 2018). Similarly, a mesocosm experiment documented bottom-up control of an aphid population, with the outcome affected by the type of light source used (Bennie et al. 2015). There are

likely negative impacts for plants dependent on nocturnal pollination services under ALAN, as these pollinators may be reduced in effectiveness or population size (Macgregor et al. 2014, Knop et al. 2017). Finally, defensive traits of plants can be under circadian regulation (Goodspeed et al. 2012) and ALAN could alter the timing of expression of these traits.

The effects of ALAN may modify local population sizes, through either top-down or bottom-up regulation, but little is known about the relative strength of artificial light effects on these two mechanisms. In one study, parasitoid wasps exerted top-down control of an aphid population under ALAN, with maximum effectiveness at low light intensity (Sanders et al. 2018). A second study described bottom-up effects on aphid populations, regulated through flower head density, and with effect size corresponding to the type of artificial light source used (Bennie et al. 2015). However, it is unclear if these effects would persist in open communities, as closed mesocosm studies do not allow for the immigration, emigration, or short-term movement of predators or herbivores. Open experiments that allow for the combined effects of altered behavior and altered local composition are rare (Sanders and Gaston 2018). In one of the few studies on the topic at the ecosystem scale, ALAN modified riparian-terrestrial nutrient fluxes over the course of a year (Meyer and Sullivan 2013), suggesting that the effects of ALAN can scale up to significantly alter ecosystem function.

Studies that investigate how artificial light alters local community composition and species interactions will be necessary to fill the current gap

in knowledge at population and community scales. Artificial light may alter community interactions through a variety of mechanisms including effects on plant tissue quality or quantity, herbivore abundance or behavior, or predator abundance or behavior. Here, we ask how artificial light affects arthropod communities, plant traits, herbivory, and predation. To characterize these effects, we conducted an open field experiment using artificial lights to assess changes in the activity-abundance and traits of arthropod communities under ALAN, as well as changes in local rates of herbivory and predation. We predicted that artificial lights would increase the local density of predators in the community, leading to stronger top-down regulation of herbivores and a decrease in herbivory under artificial lights. This *"over-compensatory predation"* hypothesis predicts that predators would aggregate in lit plots in response to allochthonous prey subsidies at night and would continue to exert consumptive or non-consumptive negative effects on herbivores during the day, decreasing overall herbivory. Alternatively, if artificial lights attracted herbivores more strongly than predators, local increases in herbivore pressure could result in an increase in total herbivore damage. This *"increased herbivory"* hypothesis would be supported if the responses of predatory taxa were unable to compensate for light-mediated increases in herbivore activity or abundance.

Methods

Summary

We monitored local mobile arthropod abundance, growth and herbivory of three plant species, and assayed predation rates under two experimental treatments – artificial light at night “ALAN” and an unilluminated control. All analyses were performed in R (version 3.5.1) (R Core Team 2017) and all plots were created with *ggplot2* and *ggmap* (Wickham 2009, Kahle and Wickham 2013).

Experimental light treatments

We illuminated plants and insect traps with artificial light at night, while others remained unilluminated as a control. We used tomato cages (65 cm tall) as a scaffold for each replicate onto which we mounted LED’s, white plastic bowls to reflect light downward, white plastic sheets to reflect light laterally, and sticky traps. Each replicate was randomly assigned one of three experimental treatments: 1) no artificial light, 2) artificial at night, or 3) artificial at night with periodic spider removal. LED lights were directed downward (12V, 3 diodes each**,** FlexFire Outdoor (IP65) UltraBright™ Design Series LED Strip Light 4200K - Natural White) and were mounted approximately 55 cm above the ground inside an overturned white plastic bowl (Figure 1). This apparatus resulted in lighting similar to the intensity and wavelengths beneath LED streetlights (Bennie et al. 2016), providing an nighttime illuminance of 749 lux at 50 cm, 167 lux at 10 cm, and 76.5 lux at ground level for ALAN treatments. The distance between plots was sufficient to isolate our lighting manipulation; adjacent control replicates had no measurable incidental lighting, with 0 lux at all heights. LED strips were

wired in parallel using 14 gauge wire, and circuits were designed to minimize voltage drop along the length of wire and minimize the amount of total wire used, resulting in 4-6 circuits in each block (Supplemental Figure 1). Within blocks, plots were arranged in a grid with 3m spacing (Figure 2).

Field site

We conducted the study within the University of California Putah Creek Reserve Experimental Ecosystem (Davis, CA, USA 38° 31.76'N, 121° 48.48'W). There are abundant invasive and native grasses and bunchgrasses (Poaceae) across most of the area with small stands of eucalyptus (*Eucalyptus* sp.), oak (*Quercus* spp.), walnut (*Juglans* sp.), almond (*Prunus* sp.), cottonwood (*Populus fremontii*), and dogwood (*Cornus* sp.) dispersed throughout. Putah Creek flows along the southern boundary of the site.

Blocks differed in terms of local vegetation and management history (Figure 2). The “basin” block (38° 31.757’N, 121° 48.556'W) was established in a long-abandoned water retention pond dominated by non-native forbs and grasses (*Centaurea* sp., *Silybum* sp., *Rumex* sp., and *Avena* sp.). The “grassland” block (38° 31.759'N, 121° 48.482'W) was established in a seasonally mowed grassland dominated by native and non-native grasses (*Elymus triticoides*, *Stipa pulchra*, *Avena* sp., and *Bromus* sp.). The “riparian” block (38° 31.686’N, 121° 48.453'W) was established in a restored grassland, approximately 30m from Putah Creek with a wider variety of herbaceous species (including *Vicia* spp., *Brassica* sp., *Avena* sp., *Elymus triticoides*, *Stipa pulchra*).

An empty 530 mL cup (SOLO brand) was installed beneath each plot and served as an epigeal live trap. This pitfall trap was filled with dead grass to allow arthropod escape in all but ALAN spider removal replicates, in which case traps were cleared of spiders every 48 hours. Experimental data were initially analyzed separately for the two illuminated treatments (ALAN and ALAN with periodic cursorial spider removal). However, nearly all response variables, including cursorial spider abundance, did not differ between the two treatments. The only response variables that differed between these two treatments were taxon-specific arthropod abundances; Lithobiomorpha, Spirobolida, Isopoda, and the family Hymenoptera-Formicidae were all reduced in abundance in the ALAN spider removal treatments compared to the ALAN treatments, but both illuminated treatments were elevated compared to control treatments. Due to the ineffectiveness of our attempts to remove spiders, these two treatments, ALAN and ALAN with spider removal (60 replicates total) were combined, hereafter simply referred to as "ALAN" and compared to 30 replicates that were unilluminated "control".

Plantings

We grew *Brassica nigra* and *Pisum sativum* seedlings in Ray Leach Cone-tainers (SC7 Stubby 3.8 cm dia, 14 cm depth, 107 ml vol, Stuewe & Sons Inc.) and obtained starts of a third species*, Solanum lycopersicum*. We transplanted 270 seedlings from the greenhouse into pre-dibbled holes underneath tomato cages, split among three blocks (30 replicates per block, each replicate with all 3 species of plants). Plants were at a median height of

10.2 cm at the time of transplants. The experiment was repeated with three cohorts of plants, transplanted into the field April 11, April 25, and May 9, 2017. Plants were surveyed for leaf number, number of leaves with insect damage, estimated area, estimated area damaged, height, and status (alive/dead) initially and after one week of experimental treatments. The second cohort of plants experienced very high drought-induced mortality due to an early-season heatwave and we excluded this cohort from all analyses of plant traits. To test hypotheses for direct effects of ALAN on plant size we applied likelihood ratio tests to linear models of plant height and plant area, each including fixed effects for treatment, cohort, block, and species. To determine if herbivory differed under ALAN, we applied a likelihood ratio test to a beta distribution glm (*package* betareg 3.1) of proportion damaged leaves (exact 0's and 1's transformed to 0.001 and 0.999 respectively). This model included fixed effects for treatment, cohort, block, and species. To determine if ALAN affected plant survival, we applied a likelihood ratio test to binomial GLM fit to plant status (live/dead) including fixed effects for treatment, cohort, block, and species.

Arthropod collection and web counts

We monitored arthropods weekly at each of the 90 replicates using 24-hour pitfall traps (530 mL cup, filled with 100 mL dilute detergent) and 48-hour sticky traps (10 cm x 20 cm translucent overhead projector sheets with both sides coated in Tanglefoot Sticky Barrier (The Scotts Company LLC). We identified individuals to order and measured body length excluding antennae

and appendages. All arthropods <1 mm length (mostly Collembela) were excluded from samples. We extended order-level identification to subdivide Hymenoptera into bees, ants, and wasps as well as separating the sub-order Homoptera from all other Hemipterans. Orders in which a large majority of taxa are known to have the potential to act as predators: Aranea, Dermaptera, Lithobiomorpha, Neuroptera, and Opilones, were counted as predators. Several frequently observed and easily identified families of predatory arthropods were also counted as predators (Carabidae - Coleoptera, Asyllidae – Diptera, Reduviidae - Hemiptera, and wasps of any taxa larger than 10 mm). All other arthropods were counted as non-predators. We aimed to capture all potential predators in our classification, regardless of primary trophic strategy. In particular, earwigs (Dermaptera), were counted as predators, and were observed acting both as nocturnal herbivores (Strauss et al. 2009) and consuming subdued flies. Counts of predator/non-predator separated by order and collection method are reported in Supplemental Figure 2.

To test for differences in the abundance of individual arthropod taxa between treatments we utilized the R function many.glm(), which accounts for multiple hypothesis testing of taxa abundance, and used a negative binomial error distribution and estimated a fixed effect for treatment (R package *mvabund* 3.13.1) (Wang et al. 2012). To determine if arthropod communities differed in either alpha or Shannon diversity underneath artificial light, we used ANOVAs including fixed effects for treatment, block,

and cohort. To test the hypothesis that artificial light altered overall abundance of arthropods we applied a likelihood ratio test to a negative binomial GLM (glm.nb – package *MASS* 7.3) including fixed effects for treatment, block, and cohort. To determine if arthropods under artificial light were more frequently predaceous we applied likelihood-ratio test to a GLM with a beta distribution describing proportion predaceous (exact 0's and 1's transformed to 0.001 and 0.999) as a function of treatment, block and cohort. Finally, to test for differences in body size between treatments, we utilized a Kolmogorov-Smirnoff tests between arthropods collected under ALAN and control treatments.

We counted volunteer spider webs on each replicate during the day, every 48 hours, but the Tetragnathid spiders that were common at this site consume their web each morning, and thus our repeated daytime counts were too low for statistical analysis. To accommodate this life history, we surveyed all replicates for spider webs on tomato cages on two nights, May 11, 2017 (riparian block only) and May 17, 2017 (all blocks) from 22:20-00:20. Only nocturnal web counts are reported. We modeled spider-web presence/absence as a function of light treatment using a binomial generalized linear model with block and cohort fixed effects.

Predation Assay

We measured the rate of predation of immobilized *Drosophila melanogaster* individuals at each plot separately during the day and the night on May 11, 2017. For each plot, we anesthetized 5 *Drosophila*

melanogaster individuals using carbon dioxide and glued their wings to a small wooden dowel (Elmer's glue – 3.15 mm diameter dowel). We placed 5 living dowel-mounted flies on the ground, tucked under the edge of each tomato cage, from 13:50-15:50 (day) and again from 22:20-00:20 (night). We counted the number of flies remaining on the dowel after 2 hours and modeled rate of predation as a function of treatment using a binomial generalized linear model with a block fixed-effect, with separate analyses for day and night data.

Results

Arthropod community

We collected, measured, and identified a total of 60,180 arthropods. Artificial light at night dramatically altered the arthropod community, with arthropod overall abundance 159% higher across ALAN replicates ($\chi^2(1)=129.44$, $p<0.001$) (Figure 3a) and 8 orders demonstrating strong positive phototaxis (Aranea: 459% increase, Coleoptera: 54% increase, Dermaptera: 2075% increase, Diptera: 335% increase, Isopoda: 270% increase, Lepidoptera: 375% increase, Lithobiomorpha: 465% increase, Opilones: 1120% increase, Orthoptera: 613% increase, Trichoptera: 1027% increase, all p-values < 0.007) (Figure 4 , Supplemental Table 1 – model summary statistics). We found no orders demonstrating significant negative phototaxis.

The effect of phototaxis on arthropod overall abundance (percent increase in arthropod abundance in ALAN treatments) was larger in sticky

traps compared with pitfall traps (interaction effect, $\chi^2(1)= 16.7$, $p<0.001$) (157% increase in sticky trap, 427% increase in pitfall trap). These effects also differed by block ($\chi^2(2)= 27.7$, $p<0.001$,) (365% increase in riparian, 58% increase in basin, 59% increase in grassland) and cohort ($p<0.001$, $\chi^2(2)= 13.6$) (54% increase in cohort 1, 227% increase in cohort 2, 59% increase in cohort 3). Notably, a fly emergence during cohort 2 at the Riparian site contributed a great deal to these treatment interactions. In our nocturnal web survey, spider web occurrence was more common on artificially lit plants ($\chi^2(1)= 3.78$, $p<0.05$, 36% ALAN treatment with webs, 20% control with webs) (Figure 4).

Arthropod composition varied significantly between ALAN and control replicates (PERMANOVA, $p<0.001$, $F(1) = 29.12$, $R^2 = 0.05$) (Figure 3e) as well as between blocks ($p<0.001$, $F(2)=5.24$, $R^2 = 0.02$) and cohorts ($p<0.001$, $F(2)=19.63$, $R^2 = 0.07$). We found higher alpha diversity in the ALAN treatment ($p<0.001$, $F(1)= 56.77$), but no difference in Shannon diversity ($p<0.95$, $F(1)= 0.00$) (Figure 3b and c). We found a higher proportion of predaceous arthropods in the ALAN treatment ($p<0.001$, $\chi^2(1)= = 13.72$, 16% predator ALAN, 8% predator control) (Figure 3d).

Many of the commonly collected orders differed in body size distribution collected under ALAN: Aranea ($p<0.001$, $D = 0.20$), Coleoptera ($p<0.001$, $D = 0.31$), Diptera ($p<0.001$, $D = 0.07$), Hemiptera (Homopterans) ($p<0.009$, $D = 0.10$), Hemiptera (non-Homopterans) ($p<0.002$, $D = 0.12$), Lepidoptera ($p<0.02$, $D=0.55$), Orthoptera ($p<0.02$,

0.35), and Trichoptera ($p<0.001$, $D = 0.78$) (Supplemental Figures 3-10). All significant orders contained larger mean size of individuals under ALAN treatments with the exception of Hemipterans (Homopteran and non-Homopteran), which were on average smaller under ALAN.

Plant size and herbivory

We found no evidence of direct effects of ALAN on plant height ($p<0.24$, $F(1)= 1.37$), plant area ($p<0.58$, $F(1)= 0.30$), or survival ($p<0.62$, $\chi^2(1)= 0.25$). We found a small indirect negative effect on plants under ALAN, with a higher proportion of leaves damaged by herbivores ($p<0.016$, $\chi^2(1)=5.83$: 34.6% leaves damaged in ALAN treatments, 28.6% leaves damaged in control) (Figure 5). A similar trend was found with percent area damaged, though not statistically significant ($p<0.366$, $\chi^2(1)=0.82$: 9.5% area damaged ALAN , 8% area damaged control). When species were separated for analysis, tomato and brassica demonstrated an elevated proportion of leaves damaged (tomato: $p<0.026$, $\chi^2(1)=4.93$, brassica: $p<0.050$, $\chi^2(1)=3.83$).

Predation experiment

We found increased fly predation rates at night under artificial light treatments ($p<0.001$, $\chi^2(1)= 63.16$, 3.65 times higher predation rates under ALAN) but found no difference in predation rates between treatments during the day ($p<0.947$, $\chi^2(1)= 0.04$) (Figure 6).

Discussion

ALAN dramatically altered arthropod abundance and composition in our experiment leading to a more diverse and predator-biased community. We found higher rates of predation on immobilized flies under ALAN at night, but not during the day. We found no direct effects of ALAN on plant size or survival but did find a small increase in the rate of herbivory. Our study found slightly larger individuals from several orders under ALAN.

Our results reinforce the importance of predator aggregation near light sources, with nearly double the proportion (15% vs 8%) of the community identified as predators under ALAN. Our predation experiment suggests that these predators are active or present primarily at night, as we saw no difference in predation rates between treatments during the day, but nighttime predation increased by 3.65 times. Previous results suggest that naïve web-building spiders prefer illuminated portions of a prey-free lab habitat, suggesting some portion of predatory taxa may be responding to the light source directly rather than a local aggregation of prey items (Heiling 1999). Finally, spiders have been shown to remain in prey-rich areas longer (Olive 1982, Bradley 1993), a distinct mechanism from phototaxis that we cannot rule out. Future studies should separate collection of arthropods between day and night collections, which could help identify attraction vs. retention as the mechanism of predator enrichment.

The observed increase in herbivory was unexpected given the increased abundance of predaceous arthropods. The increase in the proportion of leaves damaged by herbivory could be driven by changes in

plant traits, herbivore abundance, or herbivore behavior. For example, this pattern could emerge if plants under light were less defended and therefore more palatable compared to other local plants. However, a previous no-choice feeding experiment suggested that exposure to artificial lights increased the toughness of smooth brome (*Bromus inermis*) (Grenis and Murphy 2018). The increase in herbivory observed in our study would require that artificial lights changed plant traits in ways that increased their susceptibility or attractiveness to herbivores. Artificial light could have caused an increase in local abundance of herbivores or an increase in the time that local herbivores spend feeding; these changes could result from the direct effects of ALAN on herbivores themselves, or they could result if resident predators were effectively satiated by light-mediated allochtonous prey subsidies at night, leading to reduced top-down effects on local herbivores. An increase in herbivory also occur if the observed increase in predatory taxa actually included important plant-feeding omnivores as well. This explanation is consistent with our observations of European earwigs (*Forficula auricularia*) feeding aggressively on plants at night (Strauss et al. 2009).

Our observation that several orders were represented by larger individuals in ALAN treatments is consistent with previous findings that on average, orders are represented by larger individuals at night (Guevara and Avilés 2013, McMunn and Hernandez 2018). Several non-exclusive mechanisms that could explain this pattern are: 1) nocturnal arthropods

413move toward ALAN more frequently than diurnal arthropods or 2) nocturnal
414arthropods persist in the vicinity of ALAN longer than diurnal arthropods
415(Davies et al. 2012, 2017) or 3) larger individuals compete more effectively
416for high-value ALAN territory (Heiling and Herberstein 1999).

417 Our experimental results suggest that predation and herbivory happen
418more frequently under ALAN. The magnitude of the increase in nighttime
419predation was much larger than the increase in overall herbivory (265% vs
4206%), suggesting that ALAN may generally favor predaceous arthropods by
421aggregating and disorienting prey items (Acharya and Fenton 1999). Future
422studies should investigate whether this increased intensity of species
423interactions results in more total instances of herbivory or predation over the
424landscape or whether the occurrence of interactions is spatially or temporally
425aggregated. To quantify landscape level effects of ALAN, a regional
426unilluminated control should be utilized, to determine baseline rates of
427predation and herbivory compared to local control plots that may be drained
428of arthropods by ALAN. This approach, if performed at the appropriate spatial
429scale, could quantify the likely small decrease in arthropod abundance and
430species interactions in the broad areas surrounding lights. Our study further
431reinforces the importance of better understanding the spatial and temporal
432scales over which ALAN effects community and ecosystem processes (Perkin
433et al. 2011, Gaston et al. 2013). It has been suggested that one of the most
434palatable ways to mitigate impacts of ALAN on natural systems may be to
435strategically limit duration (Gaston et al. 2012), but the effectiveness of this

436method depends on the yet unmeasured speed of discovery and
437abandonment of ALAN sites by arthropods.

438 Finally we suggest future work to explore the interaction of ALAN with
439seasonal and daily temperature variation (Sanders and Gaston 2018).
440Climate change has led insects to shift seasonal and geographic ranges
441tracking beneficial thermal windows. The extent to which currently diurnal
442arthropods are capable of nighttime activity depends on other traits, in
443particular visual acuity in low light, but as organisms track a thermal window
444of activity, a portion of historically diurnal or crepuscular species may shift a
445portion of their activity to the night (Levy et al. 2018) and encounter effects
446of ALAN more frequently. This interaction between ALAN and climate change
447could be exacerbated by diurnally asymmetric warming, with nighttime
448temperatures warming more dramatically than daytime temperatures (Karl
449et al. 1991).

450 We demonstrate that differences in relative phototaxis of arthropods
451leads to dramatic changes in local community composition. This effect of
452aggregation is stronger among predators, and we see a corresponding large
453increase in the rate at which subdued prey are taken beneath ALAN. The
454effects of ALAN within communities are dramatic and complex and yet poorly
455understood. Further research, especially experiments allowing for local
456aggregation of arthropods, is needed to understand and mitigate impacts of
457ALAN on arthropod populations.

458**Acknowledgements**

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Figure 1. Schematic diagrams and photo of the apparatus used for each plot in this experiment (a-b). Each apparatus consisted of a tomato cage structure with a LED light strip affixed at the top. A white plastic bowl was used to direct the light downward onto a white plastic reflector and a slightly larger transparent acetate sticky sheet. Both sheets were suspended vertically with nylon monofilament line. A pitfall trap with a rain cover was established at the center of each plots, and three species of seedling plants

were installed in the ground around the pitfall trap during each sampling period. c) An image of an illuminated apparatus at night.

Figure 2. a) Map of experimental blocks used in this study. b-d) Each block consisted of 30 plots arranged in a 3m grid with randomized treatment assignments. White-filled points represent plots illuminated at night, and black-filled points represent plots that were not illuminated.

Figure 3 – Arthropod community summary statistics separated by treatment (ALAN and control) combined from pitfall (24-hour) and sticky traps (48-hour) (a)-d) mean values per sample +/- 1 standard error) a) total arthropod abundance b) arthropod alpha diversity per sample C) arthropod Shannon diversity per sample D) proportion arthropods sample assigned to predator category E) NMDS projection of arthropod community by treatment.

Figure 4 – Arthropod taxa displaying significant phototaxic response. Panels separated by order and displaying mean abundance by treatment (ALAN vs. control) per sample +/- 1 standard error from the total of pitfall (24-hour) and sticky (48-hour) traps. We found no examples of negative phototaxis. The degree of positive phototaxis displayed by orders varied by over an order of magnitude across taxa.

Figure 5 – Mean proportion leaves damaged by treatment +/- 1 standard error a) mean proportion leaves damaged across all plant species b) mean proportion leaves damaged - tomato only c) mean proportion leaves damaged - brassica only d) mean proportion leaves damaged - pea only. We

found a modest increase in the proportion of leaves receiving herbivory in response to ALAN overall, among tomatoes, and among peas.

Figure 6 – Mean proportion of flies eaten in predation assay +/- 1 standard error under ALAN and control replicates a) daytime assay (2 hours) b) nighttime assay (2 hours). We found a dramatic increase in nocturnal predation rates under ALAN but saw no difference in daytime predation under ALAN treatments.

Figure 1 – experiment schematic

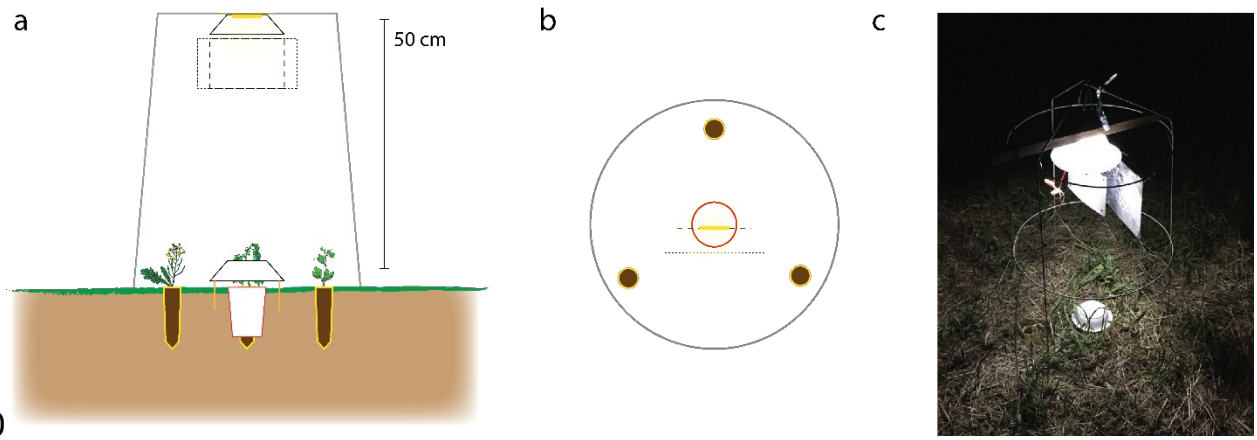
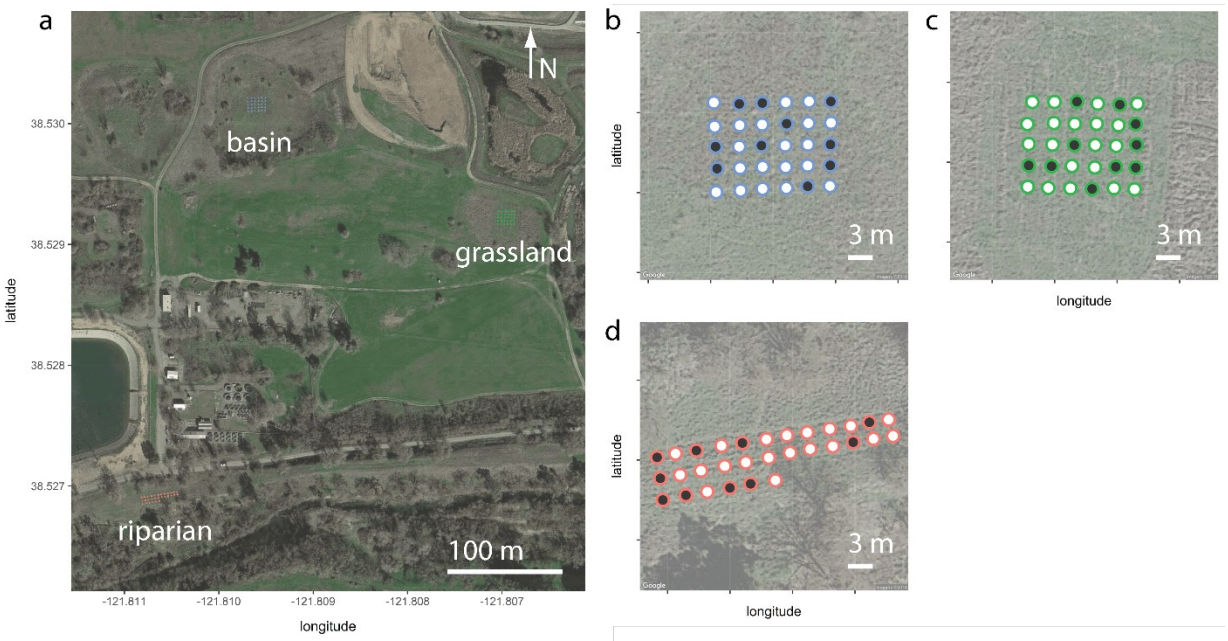


Figure 2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-121.808
-121.807
longitude
b
3 m
latitude
c
3 m
longitude
d
3 m
latitude
longitude

Figure 3

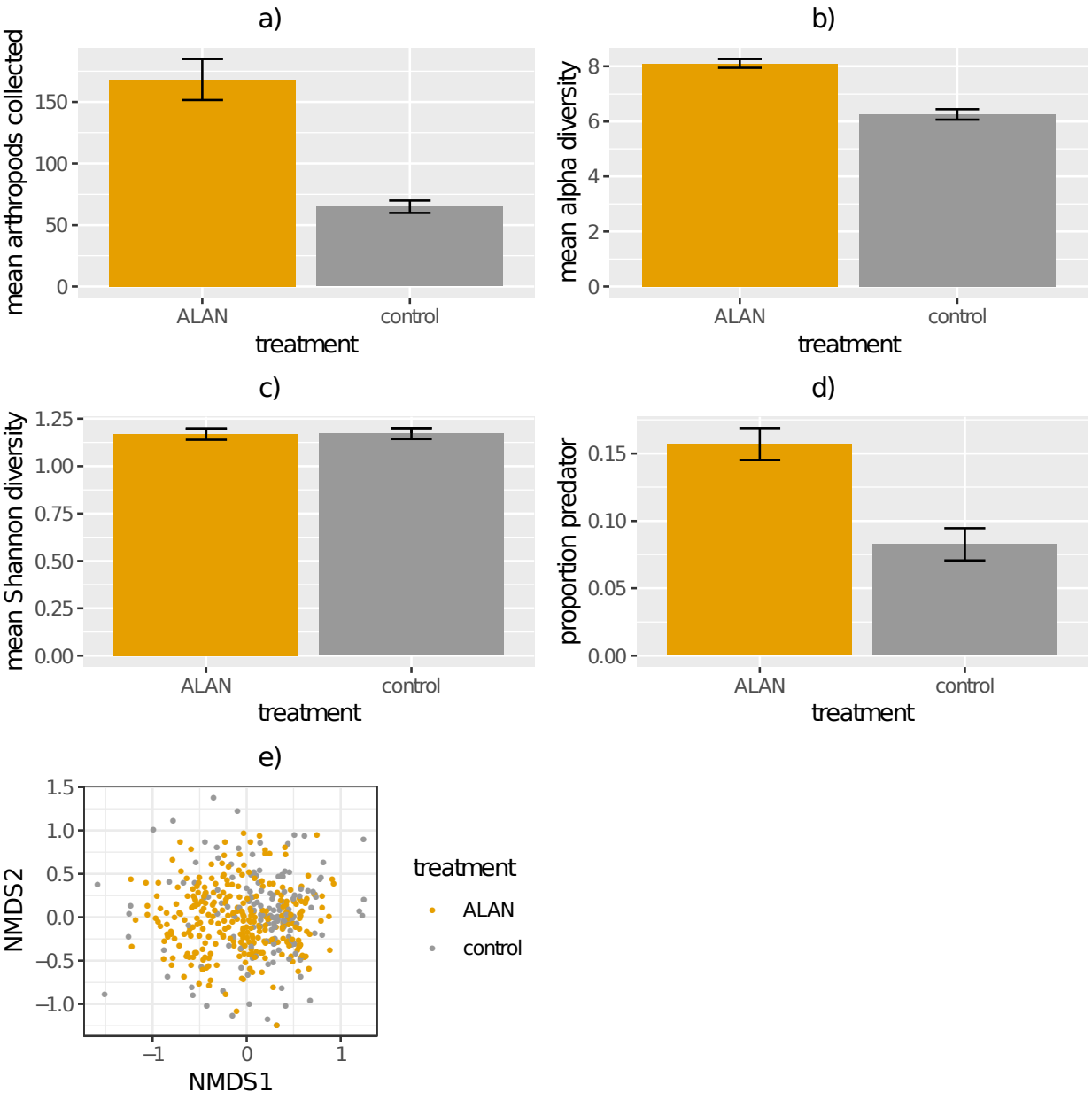

a)
mean arthropods collected
150
100
50
0
ALAN
control
treatment
b)
mean alpha diversity
8
6
4
2
0
ALAN
control
treatment
c)
mean Shannon diversity
1.25
1.00
0.75
0.50
0.25
0.00
ALAN
control
treatment
d)
proportion predator
0.15
0.10
0.05
0.00
ALAN
control
treatment
e)
NMDS2
1.5
1.0
0.5
0.0
−0.5
−1.0
−1
0
1
NMDS1
treatment
ALAN
control

Figure 4

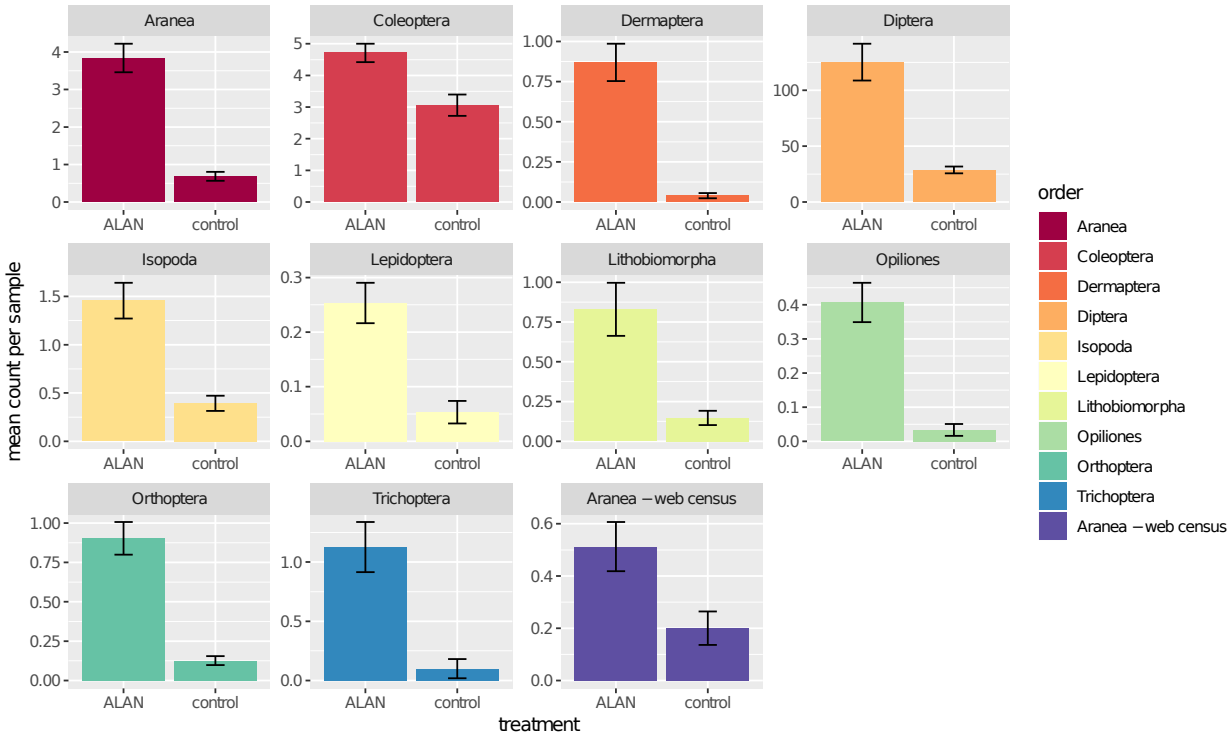

Aranea
Coleoptera
Dermaptera
Diptera
Isopoda
Lepidoptera
Lithobiomorpha
Opiliones
Orthoptera
Trichoptera
Aranea −web census
ALAN
control
mean count per sample
treatment
order

Figure 5

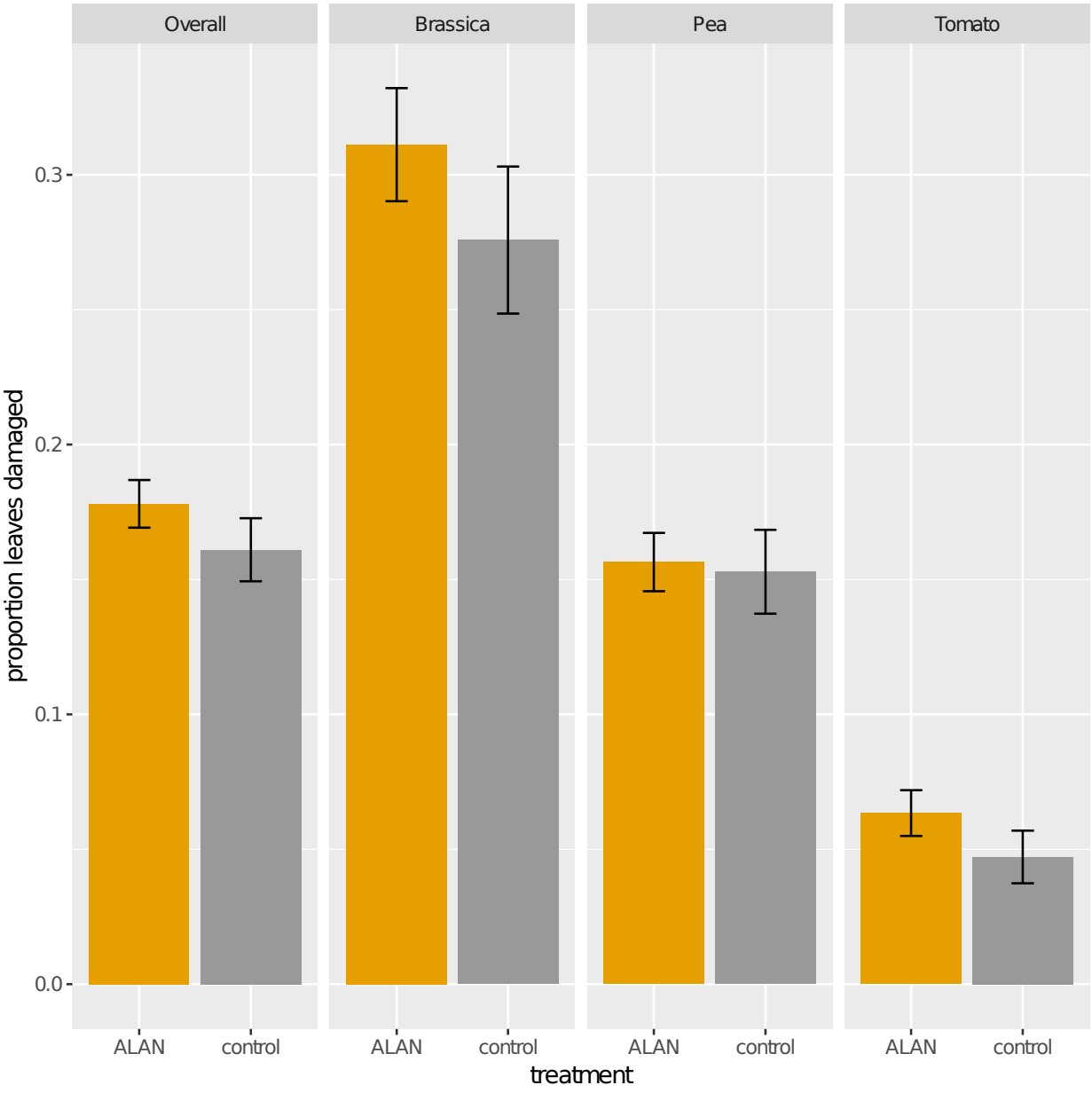
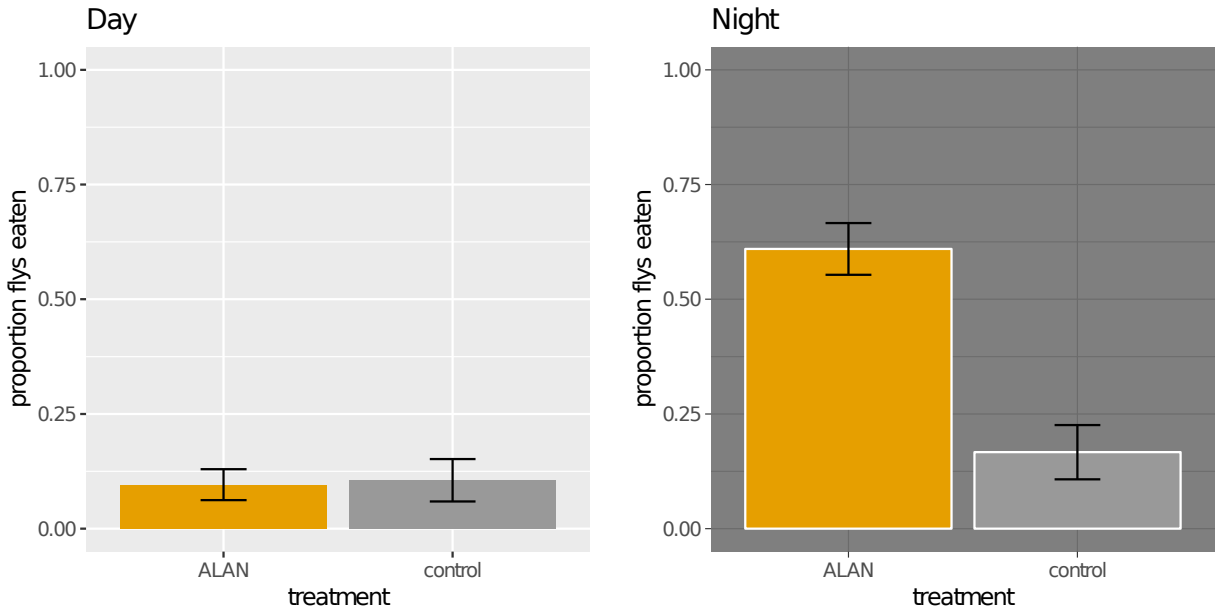

Overall
Brassica
Pea
Tomato
proportion leaves damaged
0.0
0.1
0.2
0.3
ALAN
control
treatment

Figure 6 – predation experiment



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